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Comment on Thorpe et al. 2014, *Antiquity*.

Sarah Elton, Department of Anthropology, Durham University, Durham, DH1 3LE.

Bearing in mind that modern humans, with our huge brains, complex cultures and upright walking, seem incredibly different to other living primates, it is surprisingly difficult to identify 'hominin' traits at the base of our lineage. Wood (2002) lists only a handful of features that appear to differentiate the earliest hominins from other apes – a relatively small male canine honing only at the tip, proportionately large chewing teeth, slightly larger brains, upright posture and bipedalism. The fundamental importance of bipedalism as a hominin characteristic is one obvious reason why its origins are so hotly debated. However, if reconstructing the evidence in the fossil record is akin to doing a palaeontological jigsaw, we are missing not only the picture on the box but also most of the pieces for the latest Miocene in Africa, the time period that saw the origins of our lineage. The paucity of fossil remains inevitably makes it hugely challenging to pin down the locomotor behaviour of the hominin ancestor.

Thorpe et al. (above) outline their important and compelling case for an arboreal origin of hominin bipedalism. Their theory provides an elegant explanation for the evolution of a suite of characters that make upright standing and walking – whether in the trees or on the ground – possible. The arboreal bipedalism likely to have been present in at least some Miocene apes was an exaptation that facilitated the evolution of terrestrial bipedalism. What remains a conundrum is the sequence of events that led to terrestrial bipedalism. As Paul O'Higgins and I pointed out several years ago (O'Higgins and Elton 2007), we are still some way from having a full picture of the environmental context for the evolution of hominin bipedalism, and none of the 'prime movers' or triggers currently proposed for the adoption of terrestrial bipedalism (including feeding, social behaviour, and thermoregulation) are entirely satisfactory.

Perhaps it is time that we shift focus away from seeking to explain the evolution of hominin bipedalism within polarised discussions of 'knuckle walking ancestor versus other' to consider the extent of adaptive diversity in locomotor behaviours, postures and postcrania in the Miocene ape radiation more broadly. In doing so, we may be able to consider how bipedalism fits into an array of behaviours that – we assume – are each adaptive in a particular niche and under certain contexts. Of course, this is easier said than done given the patchy nature of the Late Miocene fossil record in Africa, but this exercise would certainly be possible if the Eurasian species were considered. We need more fine-scaled and detailed studies on how small variations in postcranial morphology relate to locomotion, and how those in turn link to environment.

We may treat the type of terrestrial bipedalism evident in hominins as 'special' because of the suite of easily identifiable adaptations to it. But as Thorpe et al. (2014) state, these adaptations evolved later, after a commitment to terrestriality, and were not present in such a distinct form when the behaviour originated. Indeed, taking a broader mammalian perspective, identifying derived traits relating to locomotion in open-habitat terrestrial animals evolved from more generalist ancestral forms is not hard – the modern horse is a case in point (Wood et al. 2011). Bipedalism is also viewed as 'special' as it is one of the few features we can use to identify members of our lineage. Thorpe

and colleagues point out that given the probably ancient roots of bipedalism and the variability in arboreal bipeds, it is getting harder to use locomotion as a means of distinguishing the Hominini. By downplaying the 'special' status of bipedalism and instead considering it as one of multiple ways in which to exploit a given environment, we may be able to explore ecomorphological adaptation in more nuanced ways, and hence construct plausible scenarios that move bipedalism from the trees to the ground.

References

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